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DAILY FOOD CONSUMPTION OF *MNAIS PRUINOSA* SELYS (ZYGOPTERA: CALOPTERYGIDAE)

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Field observations were carried out at a mountain stream, some 18 km NE of Fukuoka City, Japan. The food consumption was estimated by computer simulation using the daily frequency of feeding flights and the mean weight of prey-insects collected by sticky traps. The estimates of food consumption on May 16 and 19 were 4.61 mg (min. 3.30, max. 7.67) and 5.38 mg (min. 3.61, max. 7.04) respectively. The ratios of these values to body weight amounted to 9.7% and 11.4% respectively. In addition, the daily change in stomach contents and the instantaneous rate of food output from the stomach were examined for estimating food consumption. Daily food consumption in *Sympetrum frequens*, *Calopteryx cornelia* and *M. pruinosa* was compared and a discussion is presented on the functions of the dragonfly territory, particularly on the function of the "prevention of food shortage".

INTRODUCTION

Although it is universally known that dragonflies are predators throughout their life, strikingly little is as yet known of the qualitative aspects of their feeding habits, especially in adults. HIGASHI (1973, 1979) estimated the food consumption in the adult *Calopteryx cornelia* and *Sympetrum frequens* by observing the frequency of their feeding flights and by collecting the prey-insects with sticky traps.

In the present paper an attempt is made to estimate food consumption in *M. pruinosa* by means of computer simulation, using the frequency of feeding flights and the mean weights of prey-insects of various orders, as well as the daily change in stomach contents. Also, we discuss the functions of dragonfly's territory, particularly as a means of "prevention of food shortage" (sensu MOORE, 1957).

STUDY AREA AND METHOD

The observations were carried out at a mountain stream, in the upper reaches of the Ino River (altitude 120 m above sea level), some 18km northeast of Fukuoka City, Kyushu, Japan, and which is the same area studied in previous reports (HIGASHI, 1973, 1976). The vegetation of this territory is primarily composed of intermingled plantations of Sugi (*Cryptomeria sugi*), Hinoki (*Chamaecyparis obtusa*) and Mosochiku (*Phyllostachys heterocyla*). Other plants developing along the stream are *Styrax japonica*, *Ficus erecta*, *Mallotus japonicus*, *Machilus japonica* and *Celtis sinensis*, while the herbaceous flora is mainly represented by *Polygonum cuspidatum* and *Boehemeria longispica*.

Our population studies, including observations of territorial and reproductive behaviour and estimations of daily food consumption, were carried out from April 28 to July 2, 1977. In this paper, however, we will report solely on the last aspect, which was studied in the following two ways: (1) determination of the daily change in the frequency of feeding flights and the mean weight of prey-insects in various orders collected by sticky traps, and (2) measuring of daily change in stomach contents. The detailed estimation procedure of food consumption based on (1) has been described by HIGASHI (1973, 1979). Sticky traps were adopted for collecting the prey-insects and were set in the stream whenever the observations of feeding flights of the damselfly were made. The number of prey-insects caught by the sticky traps was recorded at intervals of two hours. In order to examine the stomach contents of individual damselflies (procedure [2]), ten individuals were captured at intervals of one hour from 8:00 to 17:00 on May 16. Individuals observed during their feeding flights for 15 or 20 minutes were captured and immediately placed in sample tubes with 70% alcohol for dissection.

The instantaneous rate of food output from the stomach (IRF), which was necessary for estimating the food consumption from the daily change in stomach contents, and the daily change in the amount of faecal pellets excreted by the dragonflies, were also examined. The detailed procedures of these methods will be described in the sections concerned.

To obtain the information on the prey-insects, some dragonflies, which were seen to capture a prey were immediately collected and their prey removed. These prey-insects were placed in 70% alcohol for identification and measurement of their body weight.

RESULTS

DAILY CHANGE IN THE FREQUENCY OF FEEDING FLIGHTS

Observations of feeding flights were made simultaneously by three observers for two or three male dragonflies at intervals of one hour, and each observation time was 15 or 20 minutes. Although most of the individuals

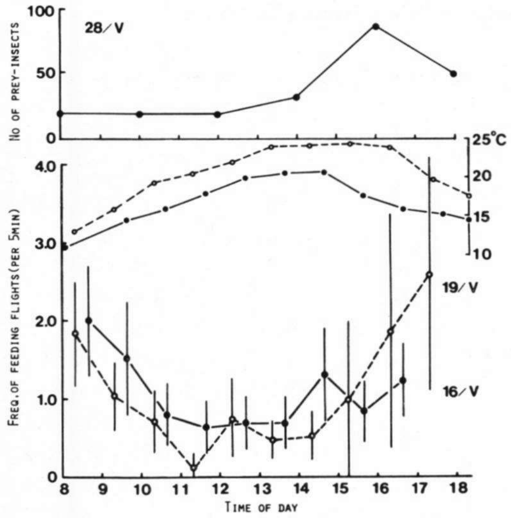

Fig. 1 Daily changes in frequency of feeding flights of *Mnais pruinosa* and in number of prey-insects collected by sticky traps. The vertical lines indicate the standard deviations.

observed were territorial males, in the early morning it could not be detected whether or not they were territorial males, because at this time the insects were usually to be found at the sunlit side of the stream on herbaceous plants growing along the forest road. The observations of feeding flights were made on May 16 and 19. The results are presented in Figure 1, where the daily changes in air temperature and in the number of the prey-insects collected by sticky traps are also shown. It is obvious, from this figure, that the frequency of feeding flights at each observation time on May 16 is larger than that on May 19, except for two observation times (15:00 and 16:00). Since the damselflies roosted about one hour earlier on May 16 than on May 19, we could not observe the feeding flights at 17:00 on this day. This phenomenon seems to have been caused by an abrupt lowering of the air temperature on the evening of the 16th. The number of prey-insects collected by sticky traps stayed at a relatively low level during the morning (before 12:00), but it increased abruptly to a high level in the evening. The frequency curves of feeding flights on both days are concave, indicating that the dragonflies feed mainly in the early morning and the evening and not so much around mid-day.

Total frequencies of feeding flights (per day) on May 16 and 19 were calculated by using the data shown in Figure 1, and the results were 117.6 times and 115.7, respectively. However, these results do not indicate the total number of feeding flights during which the prey-insects were actually captured (HIGASHI, 1973). To confirm whether or not a damselfly captured prey-insects, the movement of its mandible was observed through field glasses (x8). If mastication was recognized, the damselfly was regarded as having actually captured a prey-insect (ACP). The efficiency of capture (ECP) is given by the ratio of the frequency of successful flights to the total frequency of feeding flights. This observation was performed for several individuals whenever the circumstances permitted. Out of 186 feeding flights observed, 81 were successful, i.e. the value of ECP was 0.435. Using this value, total frequencies of ACP on May 16 and 19 were calculated, and the values of 51.2 and 50.3 respectively were obtained.

PREY-INSECTS COLLECTED BY STICKY TRAPS

A sticky tape (5 cm wide and 75 cm long) smeared on both sides with a solution of "Tangle foot" was used in the present study. A commercial name of sticky tapes is "Hae Tori Ribon" in Japan. In order to attach the tapes, a frame was made of polyester pipe (2.5cm in diameter), 1.5m high and 75cm wide. Two frames were set in the mountain stream about 10m apart. Five sticky tapes were attached horizontally to each frame at intervals of 30cm from the water surface. After leaving the tapes for 12hrs (from 7:00 to 19:00), they were removed and placed in plastic bags containing a small amount of petroleum oil. In the laboratory the insects were detached from the tapes and immersed in a petri dish with petroleum oil to wash out the Tangle foot from their body, and then placed in sample tubes with 70% alcohol for future identification. The insects were identified to the orders and the numbers of each order counted, dried at 105° C for 24hrs and weighed with an accuracy of 0.001mg using a Shimazu micro-balance. Using these results the mean weight of the insects in each order was calculated.The sticky trap observations were conducted on May 16 and 19 when the observations of feeding flights were carried out. The results are presented in Table I. It appears that the number and weight of prey-insects in each order coincide well with each other on both days.

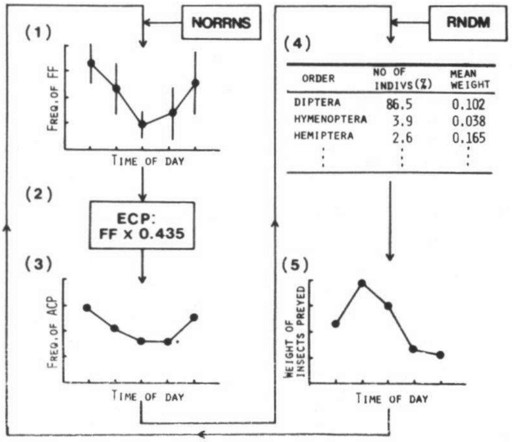

Fig. 2 Block diagram of simulation procedure for estimating the food consumption of the damselfly. NORRNS: random numbers fitting a normal distribution. RNDM: random numbers. ECP: efficiency of capturing prey-insects. FF: frequency of feeding flights. ACP: frequency of the flights by which preys are actually captured.

ESTIMATION OF FOOD CONSUMPTION BY THE SIMULATION METHOD

In order to obtain empirically the confidence intervals of these averaged values of total ACP and estimated food consumption, a computer simulation was made by using the data shown in Figure 1 and Table I. The block diagram of the simulation procedure for estimat-

Table 1
Number and mean weight of the prey-insects in each order collected by sticky traps

	May 16			*May 19*		
Order	No. of indivs.	% of total	Mean weight	No. of indivs.	% of total	Mean weight
Diptera	200	86.5	0.102	403	89.8	0.102
Hymenoptera	9	3.9	0.038	11	2.5	0.033
Hemiptera	6	2.6	0.165	13	2.9	0.154
Ephemeropter	6	2.6	0.278	6	1.3	0.543
Coleoptera	3	1.3	0.465	10	2.2	0.328
Psocoptera	2	0.9	0.004	1	0.2	0.024
Trichoptera	2	0.9	0.735	—	—	—
Thysanoptera	2	0.9	0.006	1	0.2	0.172
Neuroptera	—	—	—	1	0.2	1.342
Others	1	0.4	0.131	3	0.7	0.173
Total	*231*	*100.0*	-	*449*	*100.0*	-

ing the daily food consumption is shown in Figure 2. In this block diagram two assumptions were made: (1) the frequency of feeding flights of individuals in each time period is normally distributed (NORRNS) and (2) the prey-insects are eaten proportionally to the number of individuals caught per order, i.e. the more individuals in an order, the more are eaten. Block (1) shows the daily change in the frequency of feeding flights. From the first assumption, the frequency of feeding flights for a given individual at time t_1 can be determined randomly by the NORRNS, and also those of feeding flights at t_2, t_3, ... were determined by the same procedure. Using these results and ECP (block [2]) the frequency of ACP in each time period can be calculated for this individual (block [3]). This procedure was repeated for fifty imaginal damselflies, which constituted a unit of simulation, because two different types of random numbers (NORRNS & RNDM) were used in this diagram. The simulation was made several times starting with different initial values of these random numbers. The results are shown in Figure 3A, C.

Block (4) shows the number and weight of the prey-insects belonging to each order. From the second assumption, the number of individuals in different orders are converted into percentages of total prey-insects. The prey-insects eaten in each feeding flight were thus determined using the random numbers, and the mean weight of prey-insects of each order was used as that of prey-insects eaten (block [5]). This procedure was repeated for the frequencies of feeding flights in each time period in each individual. We could obtain the food consumption by totalling the weight of prey-insects eaten for each feeding flight and for all observation times. The estimates of food consumption for each individual on May 16 and 19 are shown in Figure 3B, D.

The estimated frequencies of ACP on May 16 and 19 were 46.6 (min. 34 - max. 60) and 51.9 (min. 33 - max. 71) respectively. From these results it is obvious that the mean and maximum frequencies of ACP on May 19 are slightly higher than those of ACP on May 16 as can be predicted from Figure 1. The estimated food consumptions on both days had mean values of 4.61 mg (min. 3.30 - max. 7.67) and 5.38 mg (min. 3.61 - max. 7.04) respectively, and agreed well with each other.

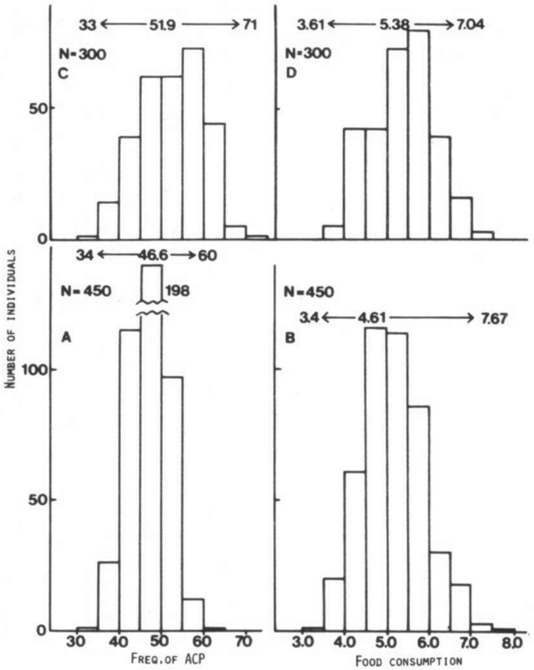

Fig. 3. Frequencies of fruitful flights (ACP) (A & C) and food consumptions (B & D) estimated by the simulation of Figure 2. The figures inscribed above the histogram indicate the mean value and ranges of min. and max. values.

EXPERIMENT ON IRF (α)

The value of IRF was obtained by the following procedure: (1) Seventy-six damselflies were captured at about 17:00, (2) they were starved separately in cages at room temperature of 24.9°C, (3) samples of ten individuals were placed in sample tubes with 70% alcohol at intervals of two hours from 18:00 to 8:00 (next day), and (4) the damselflies were dissected, the stomachs removed, then dried at 105°C for 24 hours, and weighed separately. The results are shown in Figure 4. In this figure the weights of stomach contents during the periods from 6 to 8 hours and from 10 to 14 hours after starvation were averaged and plotted at 7 and 12 hours respectively because the stomach contents of these hours were very few. A partial log-regression could be calculated between the weight of stomach contents (V) and starvation periods (t), as $\log V = -0.1826t - 0.3687$. From this equation the value of IRF (α) was obtained as 0.61 per hour. This value agreed well with a simulated value of 0.594 for *Sympetrum frequens* (HIGASHI, 1978).

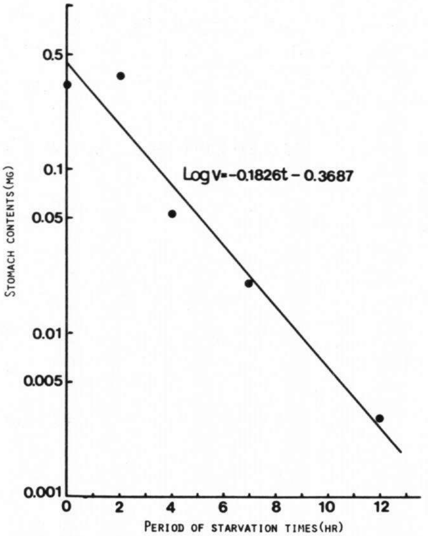

Fig. 4. Relationship between the weight of stomach contents and duration of starvation times of the damselflies.

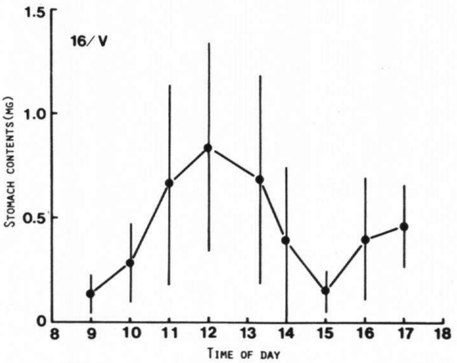

Fig. 5. Daily change in stomach contents of the damselflies (per individual). The vertical lines indicate the 95% confidence limits.

DAILY CHANGE IN THE STOMACH CONTENTS

The daily change in the stomach contents is shown in Figure 5. It can be seen from this figure that the stomach contents increased gradually from 9:00 to 12:00 and decreased from 12:00 to 15:00. They increased slightly once again between 16:00 and 17:00. From these data the daily food consumption was estimated by using the following equation of MORISITA (1971):

$$\sum_{i=1}^{n} C_{\tau i} = \alpha\tau \left\{ \sum_{i=1}^{n} V_{\tau i} - (V_0 - V_{\tau n}) \frac{e^{-\alpha\tau}}{1-e^{-\alpha\tau}} \right.$$

where $C_{\tau i}$ refers to the food consumption at respective sampling times ($i = 0, 1, 2, \ldots n$) at intervals of τ. $V_{\tau i}$ is the weight of the stomach content at each time, while V_0 and $V_{\tau n}$ stand for stomach contents at the first ($i = 0$) and the last ($i = n$) samplings respectively. The estimate of food consumption calculated by this equation was 2.05 mg per day. This estimate is about half the amount compared with that of food consumption estimated by the frequency of feeding flights. Since the proportion of food consumption to body weight was 9.7% in the latter and 4.3% in the former, and since the food consumed by *Calopteryx cornelia* was about 10% of body weight (HIGASHI, 1973), the food consumption obtained by this method may be underestimated.

This consideration may be supported by the following observation. Ten prey individuals, which were actually captured by the damselflies, were collected in the study area. The items were mayflies (3 spp.), stoneflies (2 spp., 3 specimens), three caddisflies (2 spp.) and one termite. Although smaller preys such as aphids and small diptera were frequently observed to be captured by the damselflies, we could not recover them because such small prey-insects were very quickly masticated and heavily damaged by the damselfly's mandibles. It is considered, therefore, that these collected prey-insects are among the larger insects captured.

Since the two stoneflies and the termite were not damaged, they were weighed and values of 7.8 mg, 7.3 mg and 0.6 mg respectively were obtained. It was sometimes observed that most of the wings and legs of the prey fall from the damselfly's mandible while the damselfly was masticating. Therefore we removed all the legs and wings of the two caddisflies, and determined their body weights (7.1 mg and 6.5 mg, respectively). These weights correspond approximately to the upper range of food consumption estimated by simulation (Fig. 3B, D). Although this example illustrates the case of the damselflies capturing large preys, it is expected that the weight range of stomach contents may include values of 6.5 mg to 7.1 mg. However, the mean weight of the three heavier stomach contents obtained in this study was 2.4 mg. From this observation, it is suggested also that the food consumption estimated from stomach contents is underestimated. However, it is not obvious why the weight of stomach contents is small in *Mnais pruinosa*. Further studies are needed to solve this problem.

DAILY CHANGE IN THE FAECAL PELLETS

The daily change in the faecal pellets excreted by the damselflies was examined by capturing ten individuals at intervals of two hours, and by keeping them separately for two hours in the same cylinder-cage described previously. The faecal pellets excreted by each individual during these two hours were collected, and weighed to the nearest 0.001 mg on the Shimazu micro-balance, after drying at 105°C for 24 hours. This study was performed in the same study area on June 9, 1973. The results obtained during the time from 8:00 to 18:00 were examined under natural conditions (air temperature ranged from 18.0° to 25.4°C), and those obtained from 20:00 to 8:00 (next day) were examined in the laboratory. The result is presented in Table II. The faecal pellets increased in weight gradually from 8:00 to 12:00 and maintained a constant size level from 14:00 to 18:00. The total weight of faecal pellets excreted by the damselflies per day was 3.42 mg. The food consumption can be estimated by dividing the total weight of the faecal pellets by the egestion rate.

Table II

Daily change in faecal pellets excreted by an individual *Mnais pruinosa*

1973 9 June	Time of day 8:00	10:00	12:00	14:00	16:00	18:00	20:00 -8:00	*Total*
Weight of faecal pellets (mg)	0.24	0.30	0.50	0.35	0.33	0.32	1.38	*3.42*
95% confidence limits	0.082	0.092	0.020	0.089	0.117	0.115	0.305	—
Air temperature (°C)	18.0	23.0	23.6	25.4	21.3	18.4	—	—

DISCUSSION

Some of the problems involved in the estimation of the daily food consumption in dragonflies were discussed in previous papers (HIGASHI, 1973, 1979). In the present paper, therefore, we will compare the estimated food consumptions of the three species for which the data are so far available. The results are presented in Table III. The food consumptions of *Calopteryx cornelia* and *Sympetrum frequens* obtained in 1969 were estimated by the frequency of feeding flights and the mean weight of all prey-insects collected by sticky traps, while the food consumption of *S. frequens* (Sept. 21-22, 1970) was estimated by computer simulation. The food consumptions of *S. frequens* (Sept. 22-24, 1970) and *Mnais pruinosa* (May 16, 1971), which were estimated from the stomach contents, are also shown in this table. Although the estimates of food consumption for *S. frequens* range from 10.6 mg to 12.7 mg, it is reasonable to consider that these estimates are not necessarily reflected by the differences in food consumption on each day, but that they are included in the probability range of the estimations, as can be seen in the result of simulation in which the range of estimates is 6.9-16.6 mg (mean relative error, 45.8%). The mean relative error of the estimate in *M. pruinosa* is also in the same order of magnitude (46.3%). These results mean that under the assumption made in the block diagram for computer simulation (Fig. 2) the estimates of daily food consumption fluctuate between these ranges. Therefore, from these results and the ratios of food consumption to body weight, it may be said conclusively that these three dragonfly species consume at least some 10% of their body weight as food per day.

Figure 6 shows the primary functions of dragonfly's territory which were based on the results of *Crocothemis servilia* (Higashi, unpublished), and three

Table III
Estimates of daily food consumption in three dragonfly species

Species	Date	Dry body weight (mg)	Frequency of feeding flights (times)	Food intake per day (mg)	Food intake in % of body weight
Calopteryx cornelia	1969 28, 29/VIII	64.5	62.7	6.27	11.0
Sympetrum frequens	1969 22-24/IX	84.9	159.3	11.8	13.9
	3, 5/X		172.0	12.7	15.0
	1970 21, 22/IX		148.6 (101-193)	10.6 (6.9-16.6)	12.5
	22-24/IX		—	11.5	13.5
Mnais pruinosa	1977 16/V	47.3	46.6 (34-60)	4.61 (3.40-7.67)	9.7
	19/V		51.9 (33-71)	5.38 (3.61-7.04)	11.4
	16/V		—	2.05	4.3

main functions, "copulation" (COP), "oviposition" (OVI) and "feeding" (F), are considered. Each of these refers to MOORE's definition (1957); prevention of interference with sexual behaviour, prevention of interference with oviposition and prevention of food shortage. When the circle of a function is contained in the centre of the territory's circle, it means that this function is very important with regard to territory. Consequently, when the circle of a function is completely outside the territory's circle, this function is not important as far as this dragonfly's territory is concerned. In this paper only the function "feeding" is discussed, because the results concerning "copulation" and "oviposition" are not described.

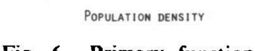

Fig. 6. Primary function of *Mnais pruinosa* territory. F, COP and OVI indicate the functions, and refer to MOORE's definitions (1957). For explanation of abbreviations see text.

JACOBS (1955) observed that males of *Perithemis tenera* only rarely feed at a pond, mating being their primary reason for appearing there. KORMONDY (1961) proposed three major functions of territory in Odonata, of which the function "to provide the male with a hunting (feeding) ground" was denied since most dragonflies at the water were mating. JOHNSON (1962), reporting on *Hetaerina americana*, denied also the function "prevention of food shortage" because swarms of small Diptera and other insects used as food were seen to be quite abundant throughout the study area for the whole season. HIGASHI (1973) reported that territorial and reproductive behaviour of *C. cornelia* was mainly observed from 10:00 to 14:00, while feeding flights were observed less frequently during this time. Similar situations were revealed in the cases of *M. pruinosa*, recorded in the present study, and *Crocothemis servilia* (Higashi, unpublished). The total frequencies of the feeding flights where prey insects were actually captured by *C. cornelia* and *M. pruinosa* were 62.7 times and 46.6-51.9 times respectively, prey-insects being captured in about 32.5% and 36.6-41.0% within the territory. On the other hand, their feeding flights were observed mainly in sunlit areas, such as forest roads or vegetation growing along forest roads in the early morning and in the evening. From these observations and from the above discussion, it can be considered that the function of "feeding" is of subsidiary importance for the dragonfly's territory, at least for those species studied.

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